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Osono, Takashi

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Takashi Osono

T. Osono

Center for Ecological Research, Kyoto University, Otsu, Shiga 520-2113 Japan

e-mail: tosono@ecology.kyoto-u.ac.jp

AbstractAn integrative survey was conducted on the ability of litter-decomposing macrofungi from forests of different climatic regions to decompose litter materials and recalcitrant compounds in the litter under pure culture conditions. A total of 75 isolates in six families of litter-decomposing macrofungi from subtropical (ST), cool temperate (CT), and subalpine (SA) forests in Japan were tested for their ability to decompose a total of eight litter types that are major substrates for macrofungi at each site. The mass loss of the litter (% original mass) during incubation for 12 weeks at 20°C ranged from -3.1% to 54.5%. Macrofungi

originated from forests of different climatic regions exhibited similar decomposing abilities, but the SA isolates caused negligible mass loss of *Abies* needles, possibly due to inhibitory compounds. Decomposing activity for recalcitrant compounds (as acid unhydrolyzable residues, AUR) was found in many macrofungal isolates. The isolates of Marasmiaceae were generally more able to cause selective decomposition of AUR than those of Mycenaceae and to decompose AUR in partly decomposed materials. The isolates of Xylariaceae had lower ligninolytic activity than those of Basidiomycetes. The AUR mass loss caused by CT isolates was significantly lower in nitrogen-rich beech litter than in its nitrogen-poor counterpart, suggesting a retarding effect of nitrogen on AUR decomposition, which was obvious for Mycenaceae. The effect of fungal family was generally more significant than that of litter type, suggesting that possible changes in the composition of fungal assemblages influence their functioning more than changes in the quality of substrates.

Keywords Acid unhydrolyzable residue · Climate · Lignin decomposition · Ligninolytic fungi · Selective delignification

35

36 **Introduction**

37

38 Fungi play central roles in decomposition processes of leaf litter because they are
39 a dominant component of soil biota and are primary decomposers of lignin and
40 other recalcitrant compounds that often limit the decomposition but which other
41 soil organisms are rarely able to mineralize. Litter-decomposing macrofungi
42 (LDM) are of particular interest in this regard, as they comprise active
43 ligninolytic species in Basidiomycota and Ascomycota (Osono 2007; Lindahl and
44 Boberg 2008; van der Wal et al. 2013). Researchers have investigated the
45 decomposing abilities of LDM with the pure culture test under laboratory
46 conditions, commonly using single litter types inoculated with several (usually
47 less than 10) LDM species associated with them (Miyamoto et al. 2000; Steffen et
48 al. 2007; Valášková et al. 2007; Boberg et al. 2011; Žifčáková et al. 2011). To the
49 knowledge of the author, few studies have compared the abilities of diverse LDM
50 to decompose multiple litter types, and compared these abilities among isolates
51 belonging to different taxa and originating from different climatic regions. I

hypothesized that the macrofungal assemblages in warmer climates included a larger number of species that had ligninolytic potential and/or that could selectively decompose recalcitrant compounds than macrofungal assemblages in cooler climates. This was based on casual observations that the decomposition of recalcitrant compounds, such as lignin, is more active in soils at warmer climates (e.g. Hirobe et al. 2004; Osono 2006; Osono et al. 2009).

The purpose of the present study was to conduct an integrative survey on the ability of LDM from forests of different climatic regions to decompose litter materials and recalcitrant compounds in the litter under pure culture conditions. A total of 75 isolates in six families of LDM from subtropical, cool temperate, and subalpine forests in Japan were tested for their ability to decompose a total of eight litter types that were major substrates for LDM at each study site. The contents of acid unhydrolyzable residues were analyzed for litter materials decomposed by LDM to investigate the ability of the LDM to decompose lignin and other recalcitrant compounds in the litter and the degree of selective decomposition of these compounds. These measures were analyzed statistically to evaluate the relative effects of fungal family, litter type, and their interaction on

69 the decomposition by macrofungi from three climatic regions.

70

71 **Materials and methods**

72

73 Study sites and collection of macrofungi

74

75 Samples were collected from three sites in Japan: a subtropical forest (ST), a cool
76 temperate forest (CT), and a subalpine forest (SA). The location, climatic
77 conditions, vegetation, and properties of the forest floor are described in Osono
78 (2014a, 2014b). Fruiting bodies of litter-decomposing macrofungi (LDM) were
79 collected from the forest floor of the study sites from March 2007 to January 2008
80 in ST, from May to November 2001 in CT, and June to October 2008 in SA (Osono
81 2014b). In the laboratory, mass spores or tissues of fruiting bodies were
82 aseptically plated onto lignocellulose agar (LCA) modified by Miura and Kudo
83 (1970) for isolation. LCA contains glucose 0.1%, KH_2PO_4 0.1%, $MgSO_4 \cdot 7H_2O$ 0.02%,
84 KCl 0.02%, $NaNO_3$ 0.2%, yeast extract 0.02%, and agar 1.3% (w/v). Note that the
85 modified LCA described by Miura and Kudo (1970) does not contain lignin or other

recalcitrant compounds. Isolates were maintained on slants of 1% malt extract agar medium [MEA, malt extract 1% and agar 2% (w/v)] at 20°C in darkness until the tests were performed.

Fungal isolates

A total of 75 isolates were used in the decomposition test to compare the decomposing ability of multiple fungal species from each study site, including 37 isolates from ST, 16 from CT, and 22 from SA (see Electronic Supplementary Material). These fungal isolates from ST, CT, and SA were inoculated to litter types collected from ST, CT, and SA, respectively (denoted as ST, CT, and SA tests). Seventy-one of the 75 isolates were obtained from mass spores or tissues of fruiting bodies during the field survey as described above. One isolate of *Marasmius* sp.ST3 was isolated from decomposing *Castanopsis sieboldii* leaves by the surface disinfection method and used for ST tests. The identification of all ST and several SA isolates to species level was not successful (Osono 2014b), and the isolates were analyzed for base sequences of the rDNAs ITS1, 5.8S, ITS2, and 28S

103 D1/D2 and assigned mostly to genus level by comparing the base sequences with
104 the GenBank database using BLAST (see ESM for the accession numbers in NIAS
105 Genebank). Three isolates (*Mycena polygramma* IFO33011, *Ampulloclitocybe*
106 *clavipes* IFO30524, and *Rhodocollybia butyracea* IFO30747) were obtained from
107 the culture collection (IFO, Osaka, Japan) and used for CT tests. These three
108 fungal species are commonly encountered in temperate regions (Imazeki and
109 Hongo 1987; Osono 2014b).
110
111 Litter materials
112
113 A total of eight litter types were used as substrata for the decomposition tests,
114 including freshly fallen leaves of seven tree species and one forest floor material.
115 The seven tree species were dominant components of forest stands and major
116 substrates for LDM in each study site (Osono 2014b). Newly shed leaves of
117 *Castanopsis sieboldii* and *Schima wallichii* without obvious fungal or faunal
118 attack were collected from the forest floor of ST in March 2008, a peak period of
119 litterfall, and used for ST tests. Newly shed leaves of *Fagus crenata* and *Quercus*

120 *crispula* without obvious fungal or faunal attack were collected from the forest
121 floor of CT in November 2002, a peak period of litterfall, and used for CT tests.
122 Specifically, leaves of *F. crenata* from the upper and lower parts of the forest slope
123 were collected separately and used for CT tests. These leaves differed in nitrogen
124 (N) content (1.32% w/w for the upper litter versus 1.75% for the lower litter),
125 mainly due to soil N availability and N use by *F. crenata* (Tateno and Takeda
126 2010). At the same time, partly decayed materials were collected from F layer at
127 the lower slope and used for CT tests. Hence, four litter types [*Fagus* (upper),
128 *Fagus* (lower), *Quercus*, and partly decomposed material] were used for CT tests.
129 Newly shed leaves of *Abies mariesii* and *Betula ermanii* without obvious fungal or
130 faunal attack were collected from the forest floor of SA in October 2008 and used
131 for SA tests. Leaves of broadleaved tree species were cut into strips 1 cm wide.
132 The leaves were oven-dried at 40°C for one week and preserved in vinyl bags until
133 the experiment was started. Tree species used as substrata are referred to as their
134 genus names in the present study for the sake of simplicity.
135
136 Pure culture decomposition test

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138 An individual pure culture decomposition test consisted of one fungal isolate
139 inoculated to one litter type, making 74 tests (37 isolates × 2 litter types) for ST,
140 64 tests (16 isolates × 4 litter types) for CT, and 44 tests (22 isolates × 2 litter
141 types) for SA. Litters (0.3 g) were sterilized by exposure to ethylene oxide gas at
142 60°C for 6 hours and used in the tests according to the methods described in
143 Osono and Hirose (2011). The sterilized litters were placed on the surface of Petri
144 dishes (9-cm diameter) containing 20 ml of 2% agar. Inocula for each assessment
145 were cut out of the margin of previously inoculated Petri dishes on 1% MEA with
146 a sterile cork borer (6 mm diameter) and placed on the agar adjacent to the litters,
147 one plug per plate. The plates were incubated for 12 weeks in the dark at 20°C.
148 The plates were sealed firmly with laboratory film during incubation so that
149 moisture did not limit decomposition on the agar. After incubation, the litters
150 were retrieved, oven-dried at 40°C for 1 week, and weighed. The initial,
151 undecomposed litters were also sterilized, oven-dried at 40°C for 1 week, and
152 weighed to determine the original mass. Four plates were prepared for each test,
153 and four uninoculated plates served as a control. Mass loss of litter was

154 determined as a percentage of the original mass, taking the mass loss of litter in
155 the uninoculated and incubated control treatment into account, and the mean
156 values were calculated for each plate. The original data are listed in ESM. Prior to
157 the tests, the sterilized litters were placed on 1% MEA, and after 8 weeks of
158 incubation at 20°C in darkness, no microbial colonies had developed on the plates.
159 Thus, the effectiveness of the sterilization method used in the present study was
160 verified. The initial litter, the control litter, and the litters with more than or
161 equal to 5.0% mass loss were used for chemical analyses as described below.
162
163 Chemical analyses
164
165 Litter materials from four replicate plates were combined to make one sample for
166 each test and ground in a laboratory mill (0.5-mm screen). The amount of
167 acid-unhydrolyzable residue (AUR) in the samples was estimated by means of
168 gravimetry as acid-insoluble residue, using hot sulfuric acid digestion (King and
169 Heath 1967). Samples were extracted with alcohol-benzene at room temperature
170 (15-20°C), and the residue was treated with 72% sulfuric acid (v/v) for 2 h at room

171 temperature with occasional stirring. The mixture was diluted with distilled
172 water to make a 2.5% sulfuric acid solution and autoclaved at 120°C for 60 min.
173 After cooling, the residue was filtered and washed with water through a porous
174 crucible (G4), dried at 105°C and weighed as AUR. This AUR fraction contains a
175 mixture of organic compounds in various proportions, including condensed
176 tannins, phenolic and carboxylic compounds, alkyl compounds such as cutins, and
177 true lignin (Preston et al. 1997).
178 Mass loss of AUR was determined as a percentage of the original mass,
179 taking the mass loss of AUR in the uninoculated and incubated control treatment
180 into account. AUR/litter mass (AUR/L) loss ratio is a useful index of the selective
181 delignification caused by each fungal species (Osono and Hirose 2009). AUR/L loss
182 ratio of each fungal species was calculated according to the equation:
183 AUR/L loss ratio = mass loss of AUR (% of original AUR mass) / mass loss
184 of litter (% of original litter mass)
185
186 Statistical analysis
187

Effects of fungal family, litter type, and the fungal family × litter type interaction on the mass loss of litter and AUR and AUR/L loss ratio were analyzed with generalized linear models (GLMs) with a Gaussian distribution for each of ST, CT, and SA tests. Only the fungal family was used as an independent variable in the GLMs to test the mass loss of AUR and AUR/L loss ratio for *Betula* litter in SA tests, because the mass loss of *Abies* litter was less than 5% for all fungal isolates tested and no AUR analysis was conducted. The GLMs were performed with the *glm* function of R version 3.0.2 for Mac (http://www.r-project.org) and with the *glht* function of the R multcomp package for multiple comparisons with Tukey's test. Paired t-test was also used to compare the mass loss of litter and AUR and AUR/L loss ratio between *Fagus* (lower) and *Fagus* (upper) litter, using JMP 6.0 for Macintosh.

Results

Litter mass loss

205 The mean mass loss of the litter caused by 37 isolates of ST tests ranged from
206 2.3% to 34.3% of the original litter mass for *Castanopsis* litter, and from -0.4% to
207 30.3% for *Schima* litter; that caused by 16 isolates of CT tests ranged from 4.1% to
208 30.2% for *Fagus* (upper) litter, from 2.3% to 29.3% for *Fagus* (lower) litter, from
209 0.1% to 42.8% for *Quercus* litter, and from 2.9% to 34.1% for partly decomposed
210 material; and that caused by 22 isolates of SA tests ranged from -3.1% to 0.6% for
211 *Abies* litter and from 0.0% to 54.5% for *Betula* litter (Fig. 1). The largest mean
212 mass loss was found for *Marasmius androsaceus* inoculated to *Betula* litter in the
213 SA test, whereas all SA isolates caused negligible mass loss of *Abies* litter.

214 In ST tests, the mass loss of litter was significantly larger for
215 Mycenaceae than for Marasmiaceae (GLM, d.f.=3, deviance=625.0, $P<0.05$; Table
216 1) and was not significantly different between *Castanopsis* and *Schima* litter
217 (GLM, d.f.=1, deviance=135.6, P=0.17; Fig. 1). The effect of fungal family × litter
218 type interaction was not significant (GLM, d.f.=3, deviance=81.1, P=0.77). In CT
219 tests, the mass loss of litter was not significantly different among fungal families
220 (GLM, d.f.=3, deviance=733.7, P=0.08; Table 1), four litter types (GLM, d.f.=3,
221 deviance=548.5, P=0.17; Fig. 1), or the fungal family × litter type interaction

(GLM, d.f.=9, deviance=973.2, P=0.46). When analyzed separately, the mean mass loss caused by the 16 CT isolates was not significantly different between *Fagus* (upper) and *Fagus* (lower) litter (paired t-test, d.f.=15, t=0.176, P=0.86), indicating that the initial N level in litter had no significant effect on fungal decomposition of the whole litter. In SA tests, the mass loss of litter was significantly affected by fungal family (GLM, d.f.=4, deviance=1007.6, $P<0.05$; Table 1), litter type (GLM, d.f.=1, deviance=4577.5, $P<0.001$; Fig. 1), and the fungal family × litter type interaction (GLM, d.f.=4, deviance=1071.5, $P<0.05$). The mass loss of *Betula* litter was generally larger for Mycenaceae than for Hymenogasteraceae (Table 1).

AUR loss

The mean mass loss of acid-unhydrolyzable residues (AUR) caused by ST isolates ranged from 0.7% to 62.6% of the original AUR mass for *Castanopsis* litter and from 0.5% to 41.0% for *Schima* litter; that caused by CT isolates ranged from 20.1% to 70.5% for *Fagus* (upper) litter, from 17.2% to 64.8% for *Fagus* (lower)

239 litter, from 7.6% to 69.4% for *Quercus* litter, and from 12.7% to 70.4% for partly
240 decomposed material; and that caused by SA isolates ranged from 0.2% to 70.6%
241 for *Betula* litter (Fig. 2). *Abies* litters inoculated with SA isolates were not
242 analyzed for AUR loss because the values of mass loss of litter caused by SA
243 isolates were negligible (Fig. 1).

244 In ST tests, the mass loss of AUR was significantly larger for Mycenaceae
245 and Marasmiaceae than for Xylariaceae (GLM, d.f.=3, deviance=2561.0, P<0.001;
246 Table 1) and was not significantly different between *Castanopsis* and *Schima*
247 litter (GLM, d.f.=1, deviance=45.8, P=0.59; Fig. 2). The effect of fungal family ×
248 litter type interaction was not significant (GLM, d.f.=3, deviance=239.8, P=0.68).
249 In CT tests, the mass loss of AUR was significantly larger for Marasmiaceae than
250 for Mycenaceae and Tricholomataceae (GLM, d.f.=3, deviance=5584.1, P<0.001;
251 Table 1) and was not significantly different among four litter types (GLM, d.f.=3,
252 deviance=83.7, P=0.94; Fig. 2). The effect of fungal family × litter type interaction
253 was not significant (GLM, d.f.=7, deviance=640.6, P=0.91). When analyzed
254 separately, however, the mean mass loss of AUR caused by CT isolates was
255 significantly lower in *Fagus* (lower) than in *Fagus* (upper) litter (paired t-test,

d.f.=14, t=2.15, P<0.05), suggesting that the higher initial N level in the lower litter suppressed fungal decomposition of AUR. Specifically, this reduction was attributed to the isolates of Mycenaceae, as the mean mass loss of AUR caused by six isolates of Mycenaceae was significantly lower in the lower litter than in the upper litter (paired t-test, d.f.=5, t=2.65, P<0.05). In contrast, no significant difference was found for the AUR mass loss between the upper and lower litter inoculated with six isolates of Marasmiaceae (paired t-test, d.f.=5, t=1.06, P=0.337). In SA tests, the mass loss of AUR in *Betula* was not significantly different among fungal families (GLM, d.f.=4, deviance=2612.1, P=0.07; Table 1).

Degree of selective decomposition of AUR

The mean AUR/L loss ratio for ST isolates ranged from 0.04 to 3.17 for *Castanopsis* litter and from 0.04 to 2.21 for *Schima* litter; that for CT isolates ranged from 1.33 to 3.70 for *Fagus* (upper) litter, from 0.93 to 3.17 for *Fagus* (lower) litter, from 1.00 to 2.00 for *Quercus* litter, and from 1.39 to 2.57 for partly decomposed material; and that for SA isolates ranged from 0.03 to 2.00 for *Betula*

273 litter (Fig. 2).

274 In ST tests, AUR/L loss ratio was significantly different among fungal
275 families (GLM, d.f.=3, deviance=11.7, P<0.001; Table 1) and was not significantly
276 different between *Castanopsis* and *Schima* litter (GLM, d.f.=1, deviance=0.02,
277 P=0.75; Fig. 3). That is, AUR/L loss ratio was significantly larger for
278 Marasmiaceae than for Mycenaceae and was significantly lower for Xylariaceae
279 than for Marasmiaceae and Mycenaceae. The effect of fungal family × litter type
280 interaction was not significant (GLM, d.f.=3, deviance=0.52, P=0.50). In CT tests,
281 AUR/L loss ratio was significantly larger for Marasmiaceae than for Mycenaceae
282 (GLM, d.f.=3, deviance=4.2, P<0.001; Table 1) and was significantly larger in
283 *Fagus* (upper) and partly decomposed material than in *Quercus* litter (GLM,
284 d.f.=3, deviance=3.4, P<0.01; Fig. 3). The effect of fungal family × litter type
285 interaction was not significant (GLM, d.f.=7, deviance=1.04, P=0.77). When
286 analyzed separately, the mean AUR/L loss ratio for CT isolates was significantly
287 lower in *Fagus* (lower) than in *Fagus* (upper) litter (paired t-test, d.f.=14, t=2.45,
288 P<0.05), indicating that the higher initial N level in the lower litter reduced the
289 degree of selective decomposition of AUR. In SA tests, AUR/L loss ratio in *Betula*

290 was significantly larger for Mycenaceae than for Tricholomataceae (GLM, d.f.=4,
291 deviance=2.7, P<0.001; Table 1).
292
293 **Discussion**
294
295 Decomposing ability of litter
296
297 The mass loss values of litter-decomposing macrofungi (LDM) in the present
298 study (Fig. 1) are within the range in previous reports of pure culture
299 decomposition by basidiomycetes (Miyamoto et al. 2000; Boberg et al. 2011;
300 Žifčáková et al. 2011) and by xylariaceous Ascomycetes (Osono et al. 2011b). The
301 results also demonstrated the stronger decomposition of litter and
302 acid-unhydrolyzable residues (AUR) by LDM than non-ligninolytic microfungi on
303 leaf litter of subtropical and tropical (Osono et al. 2008, 2009), temperate (Osono
304 and Takeda 2002; Osono et al. 2003; Koide et al. 2005; Osono et al. 2006), and
305 subalpine forests (Osono and Takeda 2006). The negligible mass loss values of
306 *Abies* needles caused by SA isolates are possibly attributable to essential oils in

307 needles that can inhibit fungal growth (Bağci and Diğrak 1996).

308

309 Fungal taxa and the decomposition of recalcitrant compounds

310

311 Decomposing activity for AUR was found in many macrofungal isolates in the
312 three sites (Figs 2 and 3), and has previously been primarily attributed to the
313 production of extracellular ligninolytic enzymes (Steffen et al. 2007; Valášková et
314 al. 2007). My data indicated that the isolates of Marasmiaceae were generally
315 better able to cause selective decomposition of AUR than those of Mycenaceae
316 (Table 1), although there was a degree of variation among the isolates. The ability
317 of Marasmiaceae to decompose AUR from partly decomposed material in CT tests
318 appeared unique as it contrasted with the abilities of Mycenaceae, which
319 exhibited reduced mass loss in partly decomposed material compared to freshly
320 fallen leaves of *Fagus* and *Quercus* (Table 1). This suggested that species in
321 Marasmiaceae are physiologically adapted to the partly decomposed materials
322 enriched in AUR, as proposed by Osono et al. (2011a). The isolates of Xylariaceae
323 in ST tests had lower ligninolytic activity than Basidiomycetes and caused

selective decomposition of components other than AUR (Table 2), in accordance with previous findings that xylariaceous fungi prefer cellulose to lignin (Nilsson and Daniel 1989). Fukasawa et al. (2009) also showed that the production by *Xylaria* species of pseudosclerotinial plates, which are insoluble to hot acid and registered as AUR, could lead to a net increase of AUR (i.e., an apparent decrease in mass loss of AUR) during pure culture decomposition.

Effect of litter quality

In CT tests, the mean value of AUR mass loss was lower in N-rich *Fagus* (lower) litter than in N-poor *Fagus* (upper) litter (Fig. 2, Table 1), suggesting a retarding effect of N on AUR decomposition. The lack of significant changes in the mass loss of whole litter (Fig. 1) indicated the enhanced decomposition of other organic components (possibly polymer carbohydrates, such as cellulose; Osono and Takeda 2001) than AUR. Such a retarding effect of N seemed more obvious for the isolates of Mycenaceae than for those of Marasmiaceae (Table 1), supporting my previous discussion that the ligninolytic system of Mycenaceae appears to be more

341 sensitive to litter quality (i.e. the content of AUR and N) than that of
342 Marasmiaceae. Laboratory experiments documented the suppression of
343 ligninolytic enzyme activities produced by basidiomycetes due to N amendments
344 (Fenn et al. 1981; Reid 1991). Similarly, excess N supply often suppressed the
345 decomposition of recalcitrant components, such as lignin, in the field (Berg and
346 Laskowski 2006; Hagiwara et al. 2012), and the activity of ligninolytic enzymes in
347 soil (Sinsabaugh et al. 2005).
348
349 Comparison of macrofungi originated from different climates
350
351 Overall, the decomposing ability for leaf litter was similar at the level of
352 macrofungal assemblage among the three study sites. This appeared
353 contradictory to the hypothesis that the decomposition of AUR in leaf litter is
354 more active in warmer than in cooler climates. This discrepancy may be explained
355 by differences in the assemblage composition of LDM, in the soil layer which LDM
356 colonized, and in temperature. First, the richness and frequency of occurrence of
357 Mycenaceae were similar among the three sites, whereas those of Marasmiaceae,

358 which included active decomposers of AUR (Table 1), were higher at warmer than
359 at cooler sites (Osono 2014b). The relative dominance of ligninolytic fungi in
360 Marasmiaceae in the macrofungal assemblage at warmer sites may be associated
361 with the more active decomposition of recalcitrant compounds in warmer than in
362 cooler climates. This is not contradictory with the finding of Osono (2011) that
363 non-ligninolytic microfungi in Ascomycetes were more frequent in surface litter at
364 cooler sites.

365 Secondly, field observations indicated that LDM mainly colonized the
366 surface L layer in ST, whereas they mainly colonized the deeper layers in CT and
367 SA (Osono 2014b). The present study demonstrated that AUR decomposition by
368 major macrofungal species in Mycenaceae was suppressed when such species
369 were inoculated to partly decomposed materials from F layer, compared to freshly
370 fallen leaves (Table 1), potentially leading to the retarded decomposition of
371 recalcitrant compounds in cooler climates. Thirdly, the higher temperatures in
372 warmer climates can enhance AUR decomposition by some ligninolytic fungi
373 (Adaskaveg et al. 1995; Osono et al. 2011c). However, how the decomposition of
374 AUR by LDM used in the present study responds to temperature and to what

375 extent the temperature-dependent response varies among the LDM isolates of
376 different origins remain unclear and should be examined in the future.
377
378 Conclusion
379
380 The pure culture decomposition tests in the present study demonstrated that
381 LDM included isolates that were capable of decomposing litter actively and
382 removing recalcitrant compounds selectively. An array of LDM thus play major
383 roles in decomposition processes and nutrient recycling on the forest floor and are
384 probably major determinants of forest productivity and matter cycling within
385 forest ecosystems of the study sites. Litter-decomposing macrofungi originated
386 from forests of different climatic regions exhibited similar decomposing abilities,
387 but the decomposing ability of LDM varied with their taxonomic position (at the
388 family level) and the type of substrate (i.e., tree species, nutrient level, and the
389 degree of decomposition). In most cases, the effect of fungal family was more
390 significant than that of litter type, suggesting that possible changes in the
391 composition of LDM assemblages influence the functioning of LDM on the forest

floor more than possible changes in the quality of substrates. This result is in accordance with the finding of Osono (2014c) and emphasizes that studying the species composition of fungal assemblages and decomposing abilities of individual fungal species is crucial for predicting the response of fungal decomposition to possible climate changes.

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Osono Table 1

Table 1. Mass loss (% original mass) of litter and AUR and AUR/litter mass (AUR/L) loss ratio caused *in vitro* by isolates of macrofungi from subtropical (ST), cool temperate (CT), and subalpine forests (SA) at 20°C for 12 weeks in darkness. Fungal isolates were inoculated to litter collected from the respective forest sites. Values are means ± standard errors for individual fungal families. Numbers of fungal isolates examined are indicated in parentheses. Nd, not determined. My, Mycenaceae; Mr, Marasmiaceae; Tr, Tricholomataceae; Hg, Hygrophoraceae; Hm, Hymenogasteraceae; Xy, Xylariaceae; Un, unidentified.

	ST				CT								SA			
	Castanopsis		*Schima*		*Fagus* (upper)		*Fagus* (lower)		*Quercus*		Partly decomposed material		*Abies*		*Betula*	
Mass loss%																
My	18.0±2.9	(15)	14.3±2.9	(15)	18.2±3.2	(6)	19.0±3.2	(6)	22.6±5.1	(6)	5.2±1.2	(6)	-1.2±0.3	(10)	26.7±4.3	(10)
Mr	12.3±1.3	(17)	9.4±1.4	(17)	18.0±4.2	(7)	16.9±3.8	(7)	22.8±6.2	(7)	16.7±4.6	(7)	-0.2	(2)	29.2	(2)
Tr	nd		nd		14.2	(2)	14.1	(2)	1.6	(2)	7.3	(2)	-0.5±0.3	(5)	11.7±7.0	(5)
Hg	nd		nd		10.5	(1)	11.0	(1)	1.4	(1)	13.8	(1)	nd		nd	
Hm	nd		nd		nd		nd		nd		nd		-0.7±0.5	(4)	4.0±2.9	(4)
Xy	10.3±2.6	(4)	13.3±3.6	(4)	nd		nd		nd		nd		nd		nd	
Un	25.7	(1)	19.0	(1)	nd		nd		nd		nd		-0.5	(1)	29.9	(1)

AUR loss%														
My	26.2±4.3	(14)	27.0±3.7	(11)	29.7±2.6	(6)	26.7±3.0	(6)	26.5±4.6	(6)	14.4±1.6	(3)	nd	43.4±6.1 (10)
Mr	26.7±3.2	(15)	21.7±3.1	(12)	46.3±7.9	(6)	43.5±8.0	(6)	45.3±9.5	(6)	49.9±7.9	(5)	nd	70.6 (1)
Tr	nd		nd		28.3	(2)	26.0	(2)	nd		14.9	(1)	nd	19.8±18.7 (3)
Hg	nd		nd		20.4	(1)	22.7	(1)	nd		26.3	(1)	nd	nd
Hm	nd		nd		nd		nd		nd		nd		nd	22.5 (1)
Xy	3.5±1.3	(4)	7.9±4.4	(3)	nd		nd		nd		nd		nd	nd
Un	30.3	(1)	17.2	(1)	nd		nd		nd		nd		nd	46.2 (1)
AUR/L loss ratio														
My	1.35±0.14	(14)	1.51±0.09	(11)	1.81±0.23	(6)	1.54±0.17	(6)	1.26±0.15	(6)	2.18±0.28	(3)	nd	1.63±0.18 (12)
Mr	1.93±0.13	(15)	1.70±0.16	(12)	2.59±0.34	(6)	2.30±0.23	(6)	1.77±0.08	(6)	2.33±0.11	(5)	nd	1.29 (1)
Tr	nd		nd		2.08	(2)	1.89	(2)	nd		1.39	(1)	nd	0.59±0.44 (3)
Hg	nd		nd		1.95	(1)	2.06	(1)	nd		1.91	(1)	nd	nd
Hm	nd		nd		nd		nd		nd		nd		nd	1.84 (1)
Xy	0.41±0.14	(4)	0.43±0.20	(3)	nd		nd		nd		nd		nd	nd
Un	1.18	(1)	0.90	(1)	nd		nd		nd		nd		nd	1.54 (1)

Figure legends

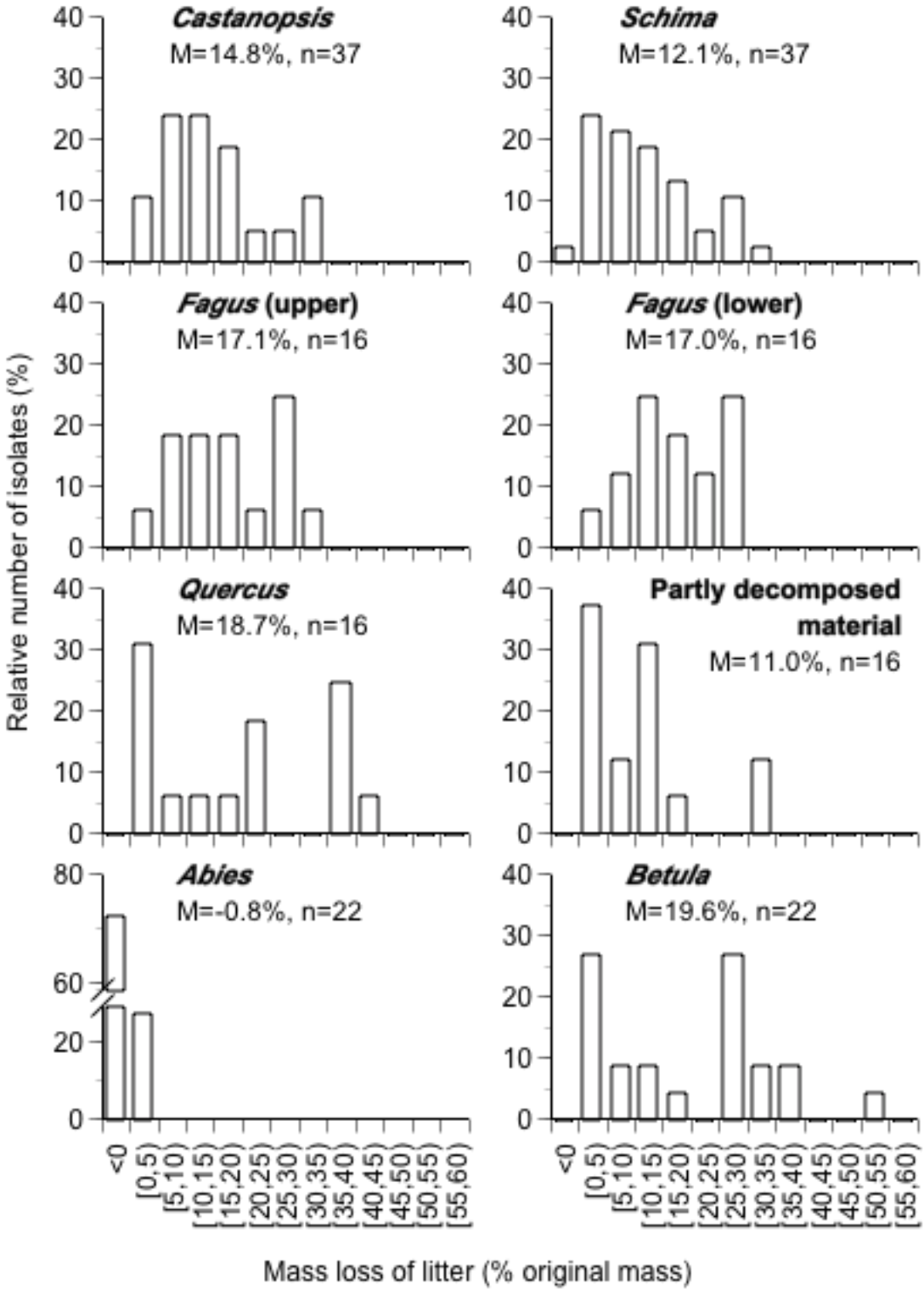
Fig. 1. Mass loss of leaf litter caused by multiple macrofungal isolates. Note that the y-axis for *Abies* litter is expanded. M, the mean value.

Fig. 2. Mass loss of acid unhydrolyzable residue (AUR) caused by multiple macrofungal isolates.

Fig. 3. Acid unhydrolyzable residue-litter loss ratio (AUR/L) of multiple macrofungal isolates.

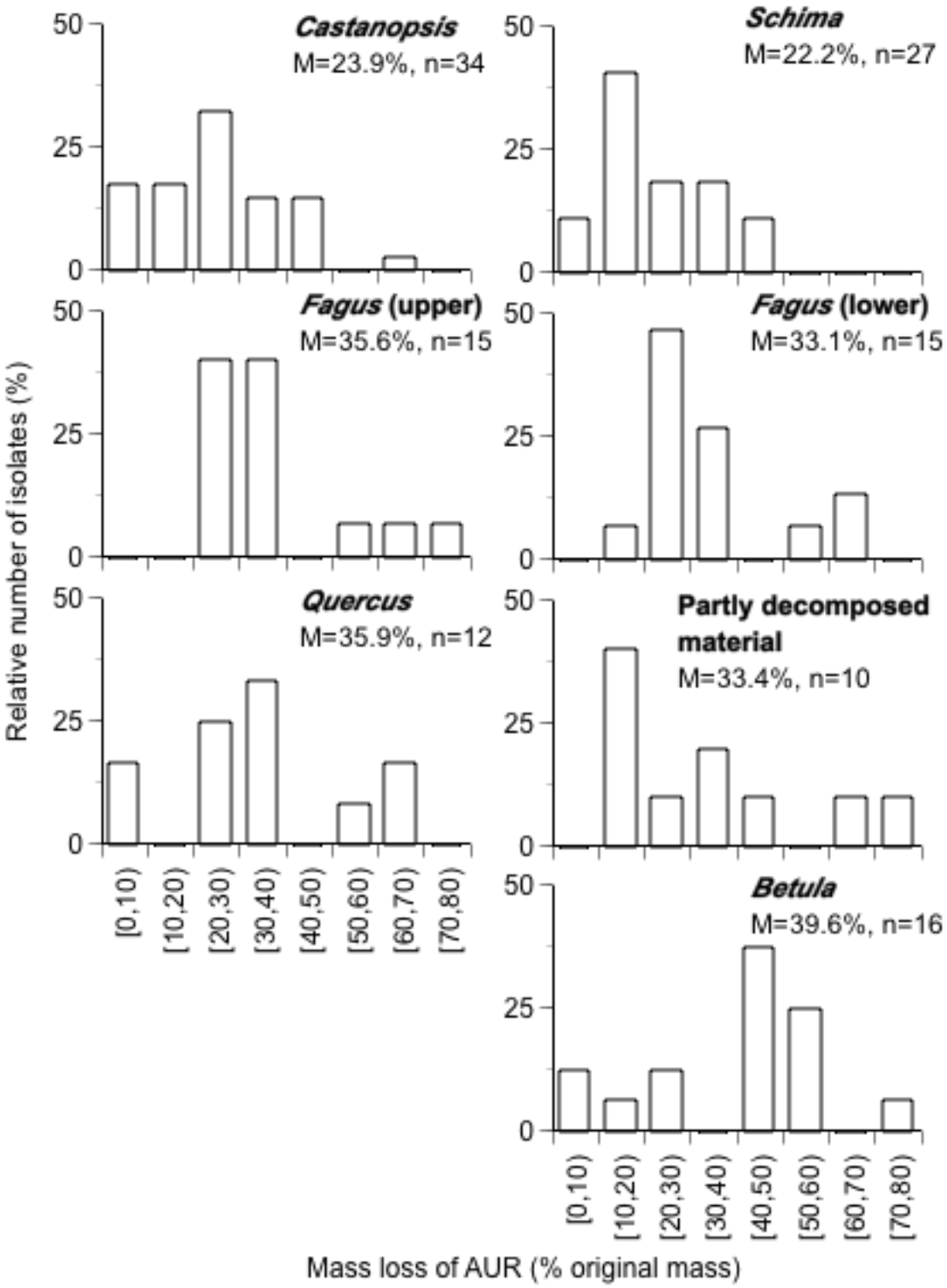
1 Osono Fig. 1

2

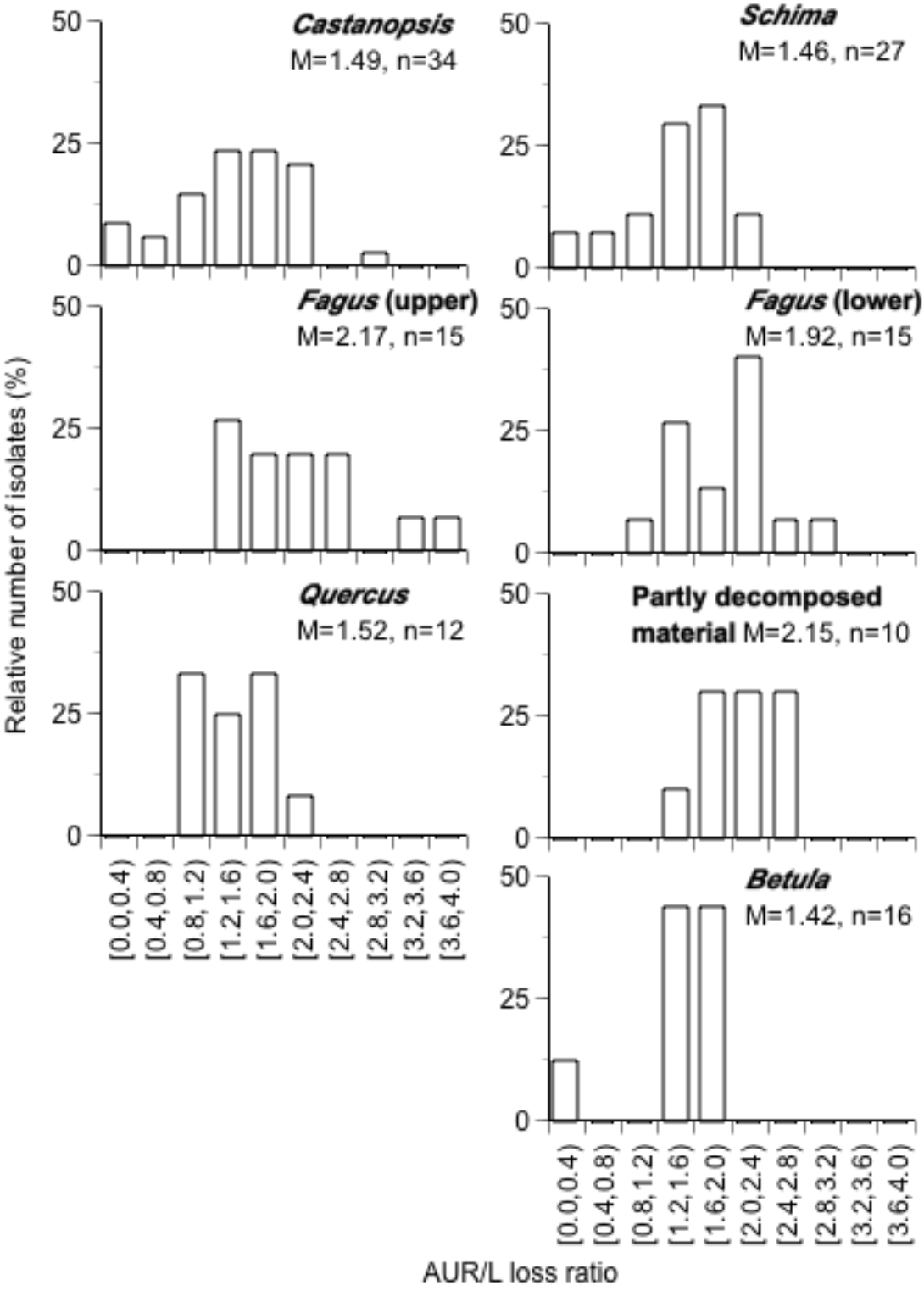


1 Osono Fig. 2

2



1 Osono Fig. 3



Electronic Supplementary Material

Decomposing ability of diverse litter-decomposer macrofungi in subtropical, temperate, and subalpine forests

Takashi Osono

S1: Mass loss (% original mass) of litter and AUR, and AUR/litter mass loss ratio (AUR/L) caused by isolates of macrofungi from subtropical (ST), cool temperate (CT), and subalpine forests (SA) at 20°C for 12 weeks in darkness. Values indicate means ± standard errors (n=4). Hy, Hygrophoraceae; Hm, Hymenogasteraceae; Mr, Marasmiaceae; My, Mycenaceae; Tr, Tricholomataceae; Xy, Xylariaceae; and Un, unidentified. nd, not determined.

Taxa	Accession	Family	Mass loss of litter	Mass loss of AUR	AUR/L	Mass loss of litter	Mass loss of AUR	AUR/L
Subtropical forest			***Castanopsis***			***Schima***		
Mycena sp. ST2	MAFF241604	My	34.3±3.6	41.7	1.22	30.3±2.1	40.2	1.32
Mycena sp. ST6	MAFF241594	My	34.2±4.4	40.6	1.19	28.1±1.9	33.1	1.18
Mycena sp. ST1	MAFF241586	My	31.5±2.2	44.8	1.42	26.7±3.1	37.4	1.40
Mycena sp. ST2	MAFF241590	My	30.6±1.4	47.2	1.54	26.9±1.2	40.9	1.52
Mycena sp. ST2	MAFF241589	My	28.8±2.0	49.2	1.71	26.1±2.9	41.0	1.57
Unidentified ST1	MAFF241593	Un	25.7±3.4	30.3	1.18	19.0±1.2	17.2	0.90

Mycena sp. ST2	MAFF241596	My	21.9±1.9	29.6	1.35	16.3±3.6	18.0	1.10
Gymnopus sp. ST3	MAFF241614	Mr	20.1±2.5	26.9	1.34	9.9±1.5	21.7	2.21
Marasmiellus sp. ST1	MAFF241613	Mr	20.0±1.2	33.0	1.65	19.9±1.6	39.4	1.98
Crinipellis sp. ST1	MAFF241601	Mr	19.7±3.6	62.6	3.17	16.4±1.3	25.2	1.54
Mycena sp. ST11	MAFF241595	My	19.3±1.9	22.9	1.19	21.2±3.0	30.6	1.44
Xylaria sp. ST1	MAFF241629	Xy	17.7±2.3	0.8	0.04	22.5±2.7	15.8	0.70
Crinipellis sp. ST1	MAFF241588	Mr	16.0±1.6	27.7	1.73	9.9±0.8	16.1	1.62
Crinipellis sp. ST2	MAFF241605	Mr	15.6±1.9	28.1	1.80	12.3±1.8	18.2	1.48
Mycena sp. ST1	MAFF241606	My	15.1±2.8	12.2	0.81	10.4±2.1	13.3	1.27
Gymnopus sp. ST1	MAFF241616	Mr	14.7±2.0	31.5	2.15	12.8±2.8	21.8	1.71
Gymnopus sp. ST4	MAFF241609	Mr	14.0±0.9	32.5	2.32	17.4±0.5	37.6	2.16
Marasmiellus sp. ST1	MAFF241610	Mr	13.8±1.6	31.2	2.25	13.4±1.4	25.7	1.91
Mycena sp. ST5	MAFF241625	My	11.9±0.8	20.0	1.68	6.0±1.2	11.2	1.86
Marasmiellus sp. ST1	MAFF241615	Mr	11.5±1.9	22.4	1.95	14.4±0.8	27.9	1.93
Gymnopus sp. ST2	MAFF241611	Mr	10.8±2.0	24.5	2.27	4.2±0.7	nd	nd
Marasmius sp. ST2	MAFF241603	Mr	10.6±2.2	19.1	1.79	6.2±0.7	12.3	1.98
Marasmius sp. ST3	MAFF241632	Mr	10.5±0.7	21.9	2.07	7.7±1.2	13.7	1.78
Mycena sp. ST8	MAFF241592	My	10.4±2.3	24.3	2.34	8.3±1.1	15.9	1.93
Marasmius sp. ST2	MAFF241602	Mr	10.0±1.3	20.7	2.08	3.8±1.4	nd	nd
Gymnopus sp. ST1	MAFF241612	Mr	10.0±1.9	14.3	1.44	2.4±0.3	nd	nd
Xylaria sp. ST1	MAFF241599	Xy	9.5±1.6	6.9	0.73	13.3±1.0	7.4	0.55

Xylaria sp. ST1	MAFF241598	Xy	8.3±2.3	4.1	0.50	12.4±1.3	0.5	0.04
Mycena sp. ST5	MAFF241626	My	8.0±2.6	10.0	1.25	2.6±2.6	nd	nd
Mycena sp. ST5	MAFF241627	My	8.0±1.9	12.0	1.49	7.4±2.2	15.2	2.06
Mycena sp. ST3	MAFF241617	My	7.3±1.4	0.7	0.09	2.3±1.0	nd	nd
Mycena sp. ST7	MAFF241628	My	7.0±2.0	11.7	1.67	2.0±0.4	nd	nd
Xylaria sp. ST1	MAFF241600	Xy	5.7±0.8	2.1	0.37	4.9±1.2	nd	nd
Marasmius sp. ST1	MAFF241591	Mr	5.0±0.8	4.9	0.98	1.1±0.9	nd	nd
Marasmius sp. ST1	MAFF241587	Mr	4.3±1.1	nd	nd	1.8±0.5	nd	nd
cf. *Calyptella* sp. ST1	Y42_07110217	Mr	3.0±0.9	nd	nd	6.9±3.0	1.0	0.14
Mycena sp. ST4	MAFF241597	My	2.3±0.3	nd	nd	-0.4±0.6	nd	nd
Cool temperate forest			***Fagus* (upper)**			***Fagus* (lower)**		
Gymnopus dryophilus	20CD_020412	Mr	30.2±1.8	70.5	2.34	27.3±1.0	64.8	2.38
Mycena polygramma	21MP_010929	My	27.7±3.9	37.4	1.35	29.3±4.0	36.1	1.23
Mycena amygdalina	17MA_0110MA	My	26.4±1.6	35.2	1.33	23.1±3.8	32.3	1.40
Gymnopus dryophilus	NBRC100095	Mr	26.3±3.1	63.7	2.42	25.2±2.1	62.4	2.47
Gerronema nemorale	24GN_010914	Mr	25.9±2.9	37.9	1.46	16.0±1.9	23.0	1.44
Rhodocollybia butyracea	19CB_000522	Mr	24.3±2.4	53.0	2.18	27.5±2.9	55.1	2.00
Mycena rorida	22MR_010903	My	18.4±0.4	30.8	1.67	18.2±0.7	31.2	1.71
Infundibulicybe gibba	NBRC100092	Tr	17.7±5.1	30.1	1.70	16.5±3.6	26.3	1.60
Mycena polygramma	IFO33011	My	16.4±4.4	24.5	1.50	23.4±3.4	21.9	0.93
Mycena crocata	15MC_0110MC	My	12.6±0.7	29.7	2.36	11.6±0.5	21.8	1.88

Pseudoclitocybe cyathiformis	18PC_0109PC	Tr	10.8±2.6	26.5	2.47	11.7±1.1	25.6	2.18
Ampulloclitocybe clavipes	IFO30524	Hy	10.5±3.6	20.4	1.95	11.0±3.2	22.7	2.06
Gymnopus peronatus	NBRC100096	Mr	9.5±0.6	32.7	3.44	10.6±0.3	33.6	3.17
Mycena amicta	16MA_0109MA	My	7.8±0.5	20.7	2.66	8.3±0.4	17.2	2.08
Marasmius pulcherripes	23MP_010929	Mr	5.4±0.9	20.1	3.70	9.4±0.9	21.9	2.33
Rhodocollybia butyracea	IFO30747	Mr	4.1±1.5	nd	nd	2.3±1.0	nd	nd
			Quercus			**Partly decomposed material**		
Gymnopus dryophilus	20CD_020412	Mr	35.8±1.7	69.4	1.94	31.0±0.8	70.4	1.91
Mycena polygramma	21MP_010929	My	38.7±2.6	38.8	1.00	3.0±1.2	nd	2.27
Mycena amygdalina	17MA_0110MA	My	35.2±2.4	36.9	1.05	3.9±2.1	nd	nd
Gymnopus dryophilus	NBRC100095	Mr	42.8±1.5	65.4	1.53	34.1±2.0	67.5	1.98
Gerronema nemorale	24GN_010914	Mr	5.0±1.6	8.7	1.76	2.9±1.0	nd	2.57
Rhodocollybia butyracea	19CB_000522	Mr	37.3±1.5	57.9	1.55	16.4±2.3	41.8	1.39
Mycena rorida	22MR_010903	My	20.7±1.0	29.0	1.40	10.8±1.1	17.5	2.54
Infundibulicybe gibba	NBRC100092	Tr	3.0±0.6	nd	nd	10.7±2.1	14.9	2.36
Mycena polygramma	IFO33011	My	21.5±3.7	22.1	1.03	2.9±1.3	nd	nd
Mycena crocata	15MC_0110MC	My	12.6±0.9	24.6	1.96	5.1±0.9	13.0	nd
Pseudoclitocybe cyathiformis	18PC_0109PC	Tr	0.1±0.4	nd	nd	3.9±1.9	nd	2.55
Ampulloclitocybe clavipes	IFO30524	Hy	1.4±1.0	nd	nd	13.8±3.3	26.3	2.27
Gymnopus peronatus	NBRC100096	Mr	20.8±0.4	38.4	1.84	14.0±0.8	35.9	nd
Mycena amicta	16MA_0109MA	My	6.8±0.8	7.6	1.12	5.4±0.3	12.7	1.62

Marasmius pulcherripes	23MP_010929	Mr	1.6±0.9	nd	nd	3.7±1.0	nd	nd
Rhodocollybia butyracea	IFO30747	Mr	16.0±1.3	31.9	2.00	14.9±2.1	33.8	nd
Subalpine forest			***Abies***			***Betula***		
Marasmius androsaceus	O14_08072204	Mr	0.6±0.7	nd	nd	54.5±1.6	70.6	1.29
Tricholomataceae sp. SA1	O23_08100702	Tr	0.0±0.4	nd	nd	39.4±2.8	57.1	1.45
Mycena sp. SA3	O20_08091705	My	-3.1±0.2	nd	nd	37.3±1.9	56.7	1.52
Mycena aurantiidisca	O2_07101503b	My	-0.3±0.3	nd	nd	32.7±1.8	41.7	1.28
Mycena epipterygia	O9_07101508	My	-2.3±1.1	nd	nd	30.9±2.2	46.5	1.50
Unidentified SA1	O17_08081203	Un	-0.5±0.5	nd	nd	29.9±2.1	46.2	1.54
Mycena epipterygia	O8_07101507b	My	-2.2±0.2	nd	nd	29.0±2.8	52.5	1.81
Mycena epipterygia	O7_07101507a	My	-0.3±0.1	nd	nd	27.8±1.6	44.5	1.60
Mycena cf. *filopes*	O11_07101510	My	-1.7±0.6	nd	nd	27.5±1.4	47.2	1.71
Mycena sp. SA2	O13_08072202	My	-0.1±0.7	nd	nd	26.5±2.1	53.0	2.00
Mycena cf. *stipata*	O24_08100703a	My	-1.0±0.3	nd	nd	25.2±3.5	44.8	1.78
Mycena aurantiidisca	O1_07101503a	My	0.0±0.2	nd	nd	18.4±1.1	29.7	1.62
Mycena cf. *stipata*	O25_08100703b	My	-1.8±0.5	nd	nd	12.2±4.9	22.5	1.84
Galerina atkinsoniana	O15_08072207	Hm	-0.9±0.6	nd	nd	12.0±1.9	17.4	1.45
Tricholomataceae sp. SA1	O10_07101509	Tr	-0.7±0.1	nd	nd	7.8±1.1	2.2	0.28
Tricholomataceae sp. SA1	O19_08091702	Tr	-1.5±0.4	nd	nd	6.4±1.7	0.2	0.03
Mycena cf. *pura*	O3_07101504	Tr	0.3±0.2	nd	nd	4.6±1.1	nd	nd
Clitocybe sp. SA1	O16_08081201	Mr	-1.0±0.6	nd	nd	3.8±1.6	nd	nd

Galerina atkinsoniana	O5_07101505b	Hm	0.1±0.4	nd	nd	3.7±2.2	nd	nd
Collybia cookei	O18_08091701	Tr	-0.6±0.1	nd	nd	0.4±0.4	nd	nd
Galerina atkinsoniana	O6_07101506	Hm	0.1±0.4	nd	nd	0.3±0.7	nd	nd
Galerina atkinsoniana	O4_07101505a	Hm	-1.2±0.3	nd	nd	0.0±0.6	nd	nd